

The Influence of Anthropogenic Disturbance and Environmental Suitability on the Distribution of the Nonindigenous Amphipod, *Echinogammarus ischnus*, at Laurentian Great Lakes Coastal Margins

Misun Kang^{1,*}, Jan J.H. Ciborowski¹, and Lucinda B. Johnson²

¹Department of Biological Sciences and
Great Lakes Institute for Environmental Research
University of Windsor
401 Sunset Avenue
Windsor, Ontario N9B 3P4

²Natural Resources Research Institute
University of Minnesota
5013 Miller Trunk Highway
Duluth, Minnesota 55811-1442

ABSTRACT. Invasion ecology offers a unique opportunity to examine drivers of ecological processes that regulate communities. Biotic resistance to nonindigenous species establishment is thought to be greater in communities that have not been disturbed by human activities. Alternatively, invasion may occur wherever environmental conditions are appropriate for the colonist, regardless of the composition of the existing community and the level of disturbance. We tested these hypotheses by investigating distribution of the nonindigenous amphipod, *Echinogammarus ischnus* Stebbing, 1899, in co-occurrence with a widespread amphipod, *Gammarus fasciatus* Say, 1818, at 97 sites across the Laurentian Great Lakes coastal margins influenced by varying types and levels of anthropogenic stress. *E. ischnus* was distributed independently of disturbance gradients related to six anthropogenic disturbance variables that summarized overall nutrient input, nitrogen, and phosphorus load carried from the adjacent coastal watershed, agricultural land area, human population density, overall pollution loading, and the site-specific dominant stressor, consistent with the expectations of regulation by general environmental characteristics. Our results support the view that the biotic facilitation by dreissenid mussels and distribution of suitable habitats better explain *E. ischnus*' distribution at Laurentian Great Lakes coastal margins than anthropogenic disturbance.

INDEX WORDS: Biological invasion, anthropogenic disturbance, environmental condition, facilitation, amphipod, dreissenid.

INTRODUCTION

Records since the early 1800s document a dramatic sequence of invasions by nonindigenous species (NIS) originating from Europe, Asia, and the North American Atlantic coast into the Laurentian Great Lakes (Mills *et al.* 1993, Grigorovich *et al.* 2003). Ballast water exchange activities of transoceanic ships have been linked with NIS introductions that originate directly from native regions and indirectly by stepwise transport from recently

colonized areas linked with the Great Lakes. Several NIS native to the Ponto-Caspian region of Eurasia (i.e., Black, Azov, and Caspian Sea basins) have expanded their range into the Great Lakes after becoming established in the Baltic Sea or lower Rhine River basins (MacIsaac *et al.* 2001). Although many NIS never establish self-sustaining populations, the movement of organisms beyond their natural range can have consequences that are ecologically and sometimes economically devastating. Consequently, considerable research has been conducted to understand why some NIS are so successful at invading while others are unsuccessful

*Corresponding author. E-mail: kang_misun@hotmail.com

(e.g., Baltz and Moyle 1993, Simberloff and Von Holle 1999, Keane and Crawley 2002, Lockwood *et al.* 2005). Studies often examine the interaction between the NIS and its new habitat and attempt to elucidate habitat attributes that make ecosystems vulnerable to invasion (e.g., Mooney and Drake 1986, Drake *et al.* 1989, Sax *et al.* 2005).

Elton (1958) observed that invasions were often human-mediated and expanded this view with the concept of "biotic resistance." He argued that the combined competitive abilities of species in undisturbed communities resist establishment of NIS, but communities disrupted or disturbed by human activities become more susceptible to invasion. Disturbance is widely regarded as a mechanism that permits NIS to avoid or reduce the intensity of biotic resistance usually manifested through interspecific competition or predation in the invaded community (e.g., Elton 1958, Hobbs and Huenneke 1992, D'Antonio 1993, Burke and Grime 1996). If disturbance is an important determinant of the success of biological invasions, it must modify species interactions or the nature of the environment in a manner that favours establishment of NIS. We use the term "stressor" in this study as a reference to anthropogenic activities that cause disturbance, defined by White and Pickett (1985) as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment."

Although a number of terrestrial studies corroborate the disturbance hypothesis (a demonstration of biotic resistance) (e.g., birds: Case 1996, plants: Kotanen 1997, Wiser *et al.* 1998, Keeley *et al.* 2003, Rose and Hermanutz 2004), relatively few studies document the importance of disturbance for NIS establishment in aquatic habitats. In manipulative experiments of the Asian kelp, *Undaria pinnatifida*, in Tasmania, Valentine and Johnson (2003) found that disturbance that reduced native algal canopy cover was critical in the establishment of this NIS, whereas the presence of a stable native algal canopy inhibited invasion. Schreiber *et al.* (2003) found that invasion of the nonindigenous snail, *Potamopyrgus antipodarum*, was facilitated by flow-driven anthropogenic disturbance, and more likely to occur in areas with multiple land uses (e.g., grazing, forestry, urban development) at lowland sites in southern Victorian Australian streams. Cohen and Carlton (1998) highlighted the role of disturbance in facilitating the establishment of NIS of the highly invaded San Francisco Bay

and delta. Except for these studies, the role of disturbance in invasion of aquatic environments has not been clearly elucidated, due to difficulty in directly linking and assessing the contribution of disturbance to invasion success.

Contrasting the disturbance hypothesis, Moyle and Light (1996) studied the success of invading fishes in California streams and suggested that if environmental factors are appropriate for a NIS, successful invasion by that species is likely, regardless of the biota already present. They argued that failure of NIS to establish in new habitats is best attributed to their inability to adapt to environmental conditions (i.e., lack of environmental suitability) rather than to biotic resistance on the part of the recipient community (also see Baltz and Moyle 1993, Harrison 1999, Hood and Naiman 2000, Fausch *et al.* 2001). Blackburn and Duncan (2001) used a global data set of historical bird introductions and showed that instances of successful introductions were not consistent with the biotic resistance hypothesis. Their model showed that the most species-rich regions of the Afrotropics and Central/South America were most invasible. Successful introductions appeared to depend on the combination of species and location (e.g., large range size, similarity of origin and introduction latitudes). Holway *et al.* (2002) compared the effects of interspecific interactions and abiotic factors on invasion success by the Argentine ant, *Linepithema humile* Mayr, in scrub habitats of southern California. Their experimental data demonstrated that community-level vulnerability to invasion appears to depend primarily on the suitability of the physical environment from the perspective of *L. humile*. Similarly, Dethier and Hacker (2005) found that physical factors played a more important role than biotic resistance in field manipulations of the invasive marine grass, *Spartina anglica*.

The objective of this study was to elucidate the factors that regulate the distribution of the non-indigenous amphipod, *E. ischnus* Stebbing, 1899, in the Laurentian Great Lakes. We assessed the influence of land-based anthropogenic activities on the distribution of the established NIS in adjacent receiving waters, to test whether disturbance as a consequence of anthropogenic activity or environmental conditions better accounted for its local occurrence. We also studied the association between *E. ischnus* and *G. fasciatus* Say, 1818, whose distribution was used as an indicator of habitat suitability for *E. ischnus* (see Study Organisms), and with dreissenids with which both amphipods have previ-

ously been found to co-occur in the Great Lakes (Griffiths 1993, Stewart and Haynes 1994, Dermott *et al.* 1998, Vanderploeg *et al.* 2002).

Evidence that *E. ischnus* is limited to relatively disturbed locations, characterized by association with anthropogenic stressors, will support the disturbance hypothesis. Alternatively, a finding of *E. ischnus* at all sites with suitable habitat (those supporting *G. fasciatus*), independent of the spatial distribution of anthropogenic stressors, will better support the hypothesis that local environmental conditions determine establishment success.

These hypotheses were evaluated by examining a subset of zoobenthic samples collected at 149 locations across the U.S. Great Lakes coastline, spanning gradients of stress, and a range of hydrogeomorphic characteristics. This study was part of the Great Lakes Environmental Indicators (GLEI) project (Danz *et al.* 2005), designed to develop and test indicators of condition along the coastal margins of the U.S. Great Lakes.

Study Organisms

Witt *et al.* (1997) reported the first account of a breeding population of the nonindigenous amphipod, *E. ischnus*, in the Great Lakes basin in 1995 at a Detroit River site. However, van Overdijk *et al.* (2003) analyzed archived samples and postulated *E. ischnus*' entry into Lake Erie in 1994 and possibly as early as 1993 (although no specimens were found in samples collected in 1993 by Dahl *et al.* [1995]). By 1996, *E. ischnus* was widely distributed from southern Lake Huron downstream to the mouth of the Niagara River of Lake Ontario (Dermott *et al.* 1998). *E. ischnus* was reported from the nearshore rocky areas of the northern to southern ends of Lake Michigan in 1998 (Vanderploeg *et al.* 2002) and nearshore silty-sand areas adjacent to Thunder Bay, Ontario in Lake Superior in 2002 (Grigorovich *et al.* 2003).

Dermott *et al.* (1998) proposed that strong eastward longshore currents in Lakes Erie and Ontario (Csanady and Scott 1974, Simons 1976, Barton and Hynes 1978) allowed *E. ischnus* to disperse from the west to the east end of Lake Erie in 2 years and permitted rapid range expansion downstream to Lake Ontario. They predicted that *E. ischnus* would quickly move downstream in the St. Lawrence River to its estuary, and enter the Mississippi River and Hudson River basins via the interconnecting canals.

The first Detroit River population was found to

occupy a habitat typical of *G. fasciatus*, suggesting the possibility of competitive displacement of the native species (Witt *et al.* 1997). As well, the proportion of *E. ischnus* increased while *G. fasciatus* decreased over a 2-year study period (1996–1997) in Port Weller, Lake Ontario, suggesting the displacement of *G. fasciatus* (Dermott *et al.* 1998).

Dermott *et al.* (1998) predicted that *E. ischnus* would replace the widespread amphipod, *G. fasciatus*, primarily on rocky substrates (i.e., wave washed cobble beaches, rubble armored shorelines, breakwalls), especially in interconnecting rivers and larger tributaries of the Great Lakes, based on observations of the rarity of *G. fasciatus* and commonness of *E. ischnus* in rocky habitats, particularly where currents were moderate, such as in the St. Clair, Detroit, and Niagara rivers. Nalepa *et al.* (2001) reported the absence of *G. fasciatus* and the sole presence of *E. ischnus* along the eastern shoreline of Lake Michigan, supporting the prediction of competitive displacement by *E. ischnus* of *G.* in rocky habitats (Dermott *et al.* 1998).

G. fasciatus is a generalist and is especially abundant in locations with dense submergent vegetation or quiet turbid areas, so is expected to continue to dominate these habitats (Dermott *et al.* 1998), although fish predation may determine relative dominance of amphipod species in rocky areas (Vanderploeg *et al.* 2002). Dermott *et al.* (1998) suggested that sites with heterogeneous substrates consisting of medium to coarse sand (gravel), silt, and submerged vegetation may be more suitable for *Gammarus* and *Hyalella* than for *E. ischnus* since these genera were found at such sites in shallow water areas of the Straits of Mackinac without *E. ischnus*. *G. fasciatus* is well equipped to cling to vegetation (Clemens 1950), and appears to be able to dominate over *E. ischnus* in turbid habitats (e.g., Canard River, Ontario), and areas with abundant submergent aquatic vegetation (Griffiths 1993).

Given that both *E. ischnus* and *G. fasciatus* are found in similar habitats in the Great Lakes, and are believed to use similar resources, habitat potentially suitable for *E. ischnus* was defined as those sites occupied by *G. fasciatus* to test the disturbance and environmental suitability hypotheses. All samples containing *Echinogammarus* was used in analyses. Sites with the presence of other amphipods, such as *Hyalella azteca* Saussure, 1858, were not considered to be suitable habitat for *E. ischnus*, because these amphipods share fewer habitat requirements (Bousfield 1958, Holsinger 1976).

METHODS

Sampling Design and Site Selection

Zoobenthic sampling locations were originally selected for the GLEI project using a stratified random design from among the entire set of 762 second-order or higher drainage basins bordering the U.S. Great Lakes coastline (Danz *et al.* 2005). The coastline was divided into coastal segments whose endpoints were midway between adjacent second order or higher tributary streams. Digital elevation models were employed to delineate the runoff areas (i.e., drainage basins) for each river basin and its adjacent shoreline. These units are referred to as “segment-sheds.” The coasts of islands, the connecting channels, and Lake St. Clair were excluded from the final site selection.

A stratified-random design was employed such that the total number of segments sampled encompassed the full range of intensity of each of six classes of stress ascertained from geospatially referenced measurements of 207 stressor variables in each drainage basin (Danz *et al.* 2005). Principal components analysis was used to reduce the total number of stressor variables to a smaller suite representing six distinct classes of anthropogenic activities: agriculture (including rates of fertilizer and agricultural chemical applications), atmospheric deposition, land use and land cover, human population density and development, point and nonpoint source pollution, and shoreline modification. The subset of segment-sheds that was ultimately sampled encompassed the full range of each of the six classes of stress (Danz *et al.* 2005). The segment-specific eigenvalue of each principal component provided a measure of the intensity of each class of stress to which the segment was subject (Danz *et al.* 2005). Our study used the five specific stressor variables that summarized most of the variability of each principal component: overall nutrient input, nitrogen and phosphorus load transported from the adjacent coastal watershed, agricultural land area, human population density, and overall pollution loading. The atmospheric deposition stressor was excluded as it stems from regional rather than local causes. An additional variable that summarized the site-specific dominant stress value (i.e., “Relmax”—the single highest principal component score of all stressor variables influencing a particular site) was also used in analyses.

Sampling locations were also classified and stratified on the basis of their hydrogeomorphologic connections with a Great Lake (following Keough

et al. 1999). These classifications are referred to as “hydrogeomorphic types.” Non-wetland areas were identified as being either high-energy shoreline, or low-energy shoreline/embayments. Three functional groups of wetlands were identified: coastal wetlands (i.e., wetlands occurring along open shorelines, unrestricted bays, or shallow, sloping beaches); river-influenced wetlands (i.e., river deltas, restricted riverine, and lake connected inland types); and protected wetlands (i.e., barrier beach systems that may be intermittently hydrologically connected to the main lake) (Keough *et al.* 1999).

Amphipods were sampled at a total of 149 sites distributed across the U.S. coastline of the Great Lakes between June and September, 2002 through 2004 (34 in Lake Superior, 42 in Lake Michigan, 28 in Lake Huron, 23 in Lake Erie, and 23 in Lake Ontario). This study uses data from 97 of these locations, and they are referred to as “basin” data. Samples from Lake Superior and protected wetlands were not included because it is unclear whether *E. ischnus* is able to persist in Lake Superior (Grigorovich *et al.* 2003) or whether *E. ischnus* has had the opportunity to disperse into wetlands that are not permanently connected to the Great Lakes shoreline. In fact, no *E. ischnus* specimens were collected from any Lake Superior sites or from protected wetlands in the GLEI study.

Additional samples collected from Lake Erie in 2004 (the Lake Erie Comprehensive Collaborative Study [ECCS], Krieger *et al.* in press) supplemented the GLEI Lake Erie high-energy shoreline data. Amphipods were collected from 96 sampling locations along the U.S. coastline of Lake Erie between May and Sept 2004 using an airlift sampler (314 cm²; stony substrates) or Ponar grab (506 cm²; soft substrate sampler; see Krieger *et al.* (2007) for a full description of their methods). Only those sites that were sampled along the U.S. coastline could be used in our analyses because appropriate stressor scores are not currently available for segment-sheds on Canadian Great Lakes coastlines.

Amphipod Collection

Using a combination of 30-s D-net, 10-cm deep, 6.5-cm diameter cores, and Petite Ponar grabs (225 cm²; or rock scrapes of equivalent top-face surface area in rocky habitats), we collected duplicate samples at two to four depth locations along each of two to six transects per site. Two to three transects were delineated extending from each of the two most common land use classes that made up at least

10% of the linear extent of the shoreline. High-energy and coastal wetland benthic samples were collected at four depth contours along each transect: 20–50 cm, 50–75 cm, 5 m (or 1 km from shore, whichever occurred first), and 10 m (or 2 km from shore, whichever occurred first). If depths were 5 m or less, only three locations were sampled along a transect at embayments, river-influenced wetlands, and protected wetlands (20–50 cm, 50–75 cm, deepest point encountered); a maximum of 24 points was sampled at each site. All samples were preserved in 2.5:1 v/v ethanol: buffered formalin solution diluted 1:1 with lake water, and sorted in the laboratory.

In the laboratory, one randomly selected sample of each duplicate from each zone of each transect was sorted. Benthic samples were rinsed through a series of nested sieves (4 mm, 1 mm, 0.5 mm, 0.25 mm) following the procedures of Ciborowski (1991). Individual size fractions were subsampled as necessary to generate at least 100 invertebrates per fraction such that the total sorting time spent per sample did not exceed 3 hours. Similar methods were used for processing ECCS samples (see Krieger *et al.* 2007). Amphipods were identified to the genus level using the key of Covich and Thorp (2001). *Gammarus* species were identified using keys of Holsinger (1976) and Bousfield (1958). *E. ischnus* specimens were identified using the description outlined by Witt *et al.* (1997).

Statistical Analyses

The association between *E. ischnus* and *G. fasciatus* was examined to complement the tests of the disturbance hypothesis and environmental suitability hypothesis of invader establishment at individual sites with suitable habitat. The associations were examined using frequency analyses (Yates corrected Chi-square analysis of presence/absence data, with one degree of freedom). Differences in degree of co-occurrence among lakes and hydrogeomorphic types were assessed using heterogeneity tests. A taxon was deemed present at a site if one or more individuals occurred in at least one sample. A significant positive association between two taxa was assumed to indicate that the taxa pair shared similar habitats (e.g., hydrogeomorphic types). A nonsignificant Chi-square outcome would imply that the broad distributions of the two taxa were independent of one another. Strongest support for the environmental suitability hypothesis would be achieved if *E. ischnus* was detected wherever *G.*

fasciatus was encountered, and independently of the anthropogenic stressor scores.

Dreissena polymorpha Pallas, 1771, and *Dreissena bugensis* Andrusov, 1897, are two nonindigenous dreissenid species that occur in the Great Lakes. Given that dreissenids are known to form mixed-species colonies (Bially and MacIsaac 2000) and have been shown to be associated with *E. ischnus* and *G. fasciatus* (Griffiths 1993, Stewart and Haynes 1994, Dermott *et al.* 1998, Vanderploeg *et al.* 2002), frequency analyses (Yates corrected Chi-square analysis of presence/absence data, with one degree of freedom) were also conducted to quantify the strength of association between dreissenids and each gammarid taxon. Dreissenids were collected using the same methods as for amphipod collection.

To test the disturbance hypothesis, simple and multiple logistic regression analyses were performed on occurrence records for *E. ischnus* data at sites from which *G. fasciatus* were also collected. *E. ischnus* presence/absence (coded 1/0, respectively) site values were regressed against the principal component scores for each of the six stressor variables using simple logistic regression. Multiple logistic regression analysis evaluated the simultaneous effect of the five single stressor measures. The Relmax stressor variable was not included in the multiple regression analysis since it already combines effects of the various stressors. We anticipated that a logistic regression analysis approach would allow us to estimate theoretical critical/threshold stressor scores for *E. ischnus* occurrence (the stressor score at which *E. ischnus* is more than 50% likely to occur).

We used a hierarchical approach to test the hypotheses. Data were examined at the basin scale, lake-by-lake, by coastal hydrogeomorphic type, and finally, at the microhabitat (individual sample location) scale.

A modified Bonferroni correction (Holm 1979) was used to adjust the study-wide Type I error to 0.05. All analyses were performed using the Statistica® software package Version 6.0 (StatSoft, Inc. 2001).

RESULTS

Distribution and Associations among Taxa

G. fasciatus was the predominant species of *Gammarus* collected, although *G. tigrinus* Sexton, 1939 (new records for the Great Lakes in Grigorovich *et al.* 2005), and *G. pseudolimnaeus* Bous-

TABLE 1. Representation of sites with presence of *E. ischnus* (*E*), *G. fasciatus* (*G*), and *Dreissena* spp. (*D*). Arrows indicate whether a taxon was collected more frequently (\uparrow) or less frequently (\downarrow) than expected if distribution was random across all sites at a given scale. Numbers given show percentage of expected frequency.

Scale	E (%)	G (%)	D (%)
Michigan	\downarrow 52.4	\downarrow 96.7	\downarrow 69.9
Huron	\downarrow 78.6	\downarrow 89.8	\uparrow 116.6
Erie	\uparrow 182.5	\downarrow 89.8	\uparrow 108.2
Ontario	\uparrow 170.0	\uparrow 129.7	\uparrow 134.7
Coastal wetland	\downarrow 72.9	\uparrow 109.1	\downarrow 97.4
Embayment	\uparrow 136.1	\downarrow 71.9	\uparrow 121.2
High-energy	\uparrow 136.1	\downarrow 53.9	\uparrow 121.2
River-influenced wetland	\downarrow 63.8	\uparrow 164.7	\downarrow 63.1

field, 1958, were also found in samples. Our power for detection of species weakened for analyses performed at smaller spatial scales for which there were smaller sample sizes (Lakes Erie and Ontario and specific hydrogeomorphic types). The sample sizes of the basinwide ($n = 97$ without Lake Superior and protected wetlands), Lakes Michigan ($n = 39$), Huron ($n = 26$), ECCS Lake Erie ($n = 96$), high-energy ($n = 30$), and coastal wetland ($n = 28$) scales provided suitable α -levels (0.75) for detection of rare species (as per McArdle 1990). The small sample sizes of Lakes Erie ($n = 14$), Ontario ($n = 18$), embayments ($n = 15$), and river-influenced wetlands ($n = 24$) resulted in analyses with low power to detect rare species. However, *E. ischnus* had its highest frequency of occurrence in Lakes Erie and Ontario (comprising 26% and 32%, respectively, of all Great Lakes sites at which *E. ischnus* occurred).

Based on its basinwide frequency of occurrence among sites, *E. ischnus* was under-represented in Lakes Michigan, Huron, coastal, and river-influenced wetlands, and over-represented in Lakes Erie, Ontario, high-energy, and embayment sites (Table 1).

G. fasciatus was collected more frequently in Lake Ontario, and river-influenced wetlands, and was more under-represented in high-energy and embayment sites than would be expected by chance if they were randomly distributed across the Great Lakes (Table 1).

Dreissena spp. mussels followed the same pattern

of frequency as *E. ischnus* but were also over-represented in Lake Huron (Table 1).

E. ischnus-*G. fasciatus* Co-occurrence

G. fasciatus was found at 54 of the 97 GLEI sites sampled (56%) (Fig. 1). *E. ischnus* was found at 19 of the 97 sites sampled (20%) (Fig. 1), and occupied 26% of the *G. fasciatus* sites. *E. ischnus* was found without *G. fasciatus* at only five locations: one embayment in Lake Huron, and at two high-energy sites in each of Lakes Michigan and Erie. Although the number of sites with co-occurrence was higher than would be expected by chance (132%), the association between *E. ischnus* and *G. fasciatus* at the basin level was not statistically significant ($\chi^2 = 2.27$, d. f. = 1, $p > 0.05$; Table 2). Tests for association at the scales of individual lakes, and hydrogeomorphic types, were also nonsignificant (Table 2). There was also no significant among-lake heterogeneity in the degree of association between *E. ischnus* and *G. fasciatus* ($p > 0.05$). However, there was significant heterogeneity in the degree of co-occurrence among the hydrogeomorphic types ($p < 0.001$). The distributions of *E. ischnus* and *G. fasciatus* deviated significantly from expectation of independence at high-energy and river-influenced sites ($p < 0.005$ and $p < 0.001$, respectively) due to their respective over-representation in these types of sites.

There was a highly significant association between the two gammarid species at the microhabitat (individual sample location) scale ($\chi^2 = 27.32$, $p < 0.0005$, $n = 925$; Table 2). The number of samples in which *E. ischnus* and *G. fasciatus* co-occurred was much higher than what would be expected by chance.

Analyses of the ECCS data failed to show significant association between *E. ischnus* and *G. fasciatus* distributions for Lake Erie ($\chi^2 = 0.38$, $p > 0.05$, $n = 96$; Table 2). *E. ischnus* was found at 19 of the 96 sites sampled (20%) (Table 2), and overlapped at 5% of the *G. fasciatus* sites. Thirteen sampling locations occupied by *E. ischnus* were not occupied by *G. fasciatus*.

Distribution of *E. ischnus* across Stressor Gradients

The geographic extent and range of stress covered by the 97 GLEI sites that we sampled is suitable to test the disturbance and the environmental suitability hypotheses (Fig. 2). *E. ischnus* sites

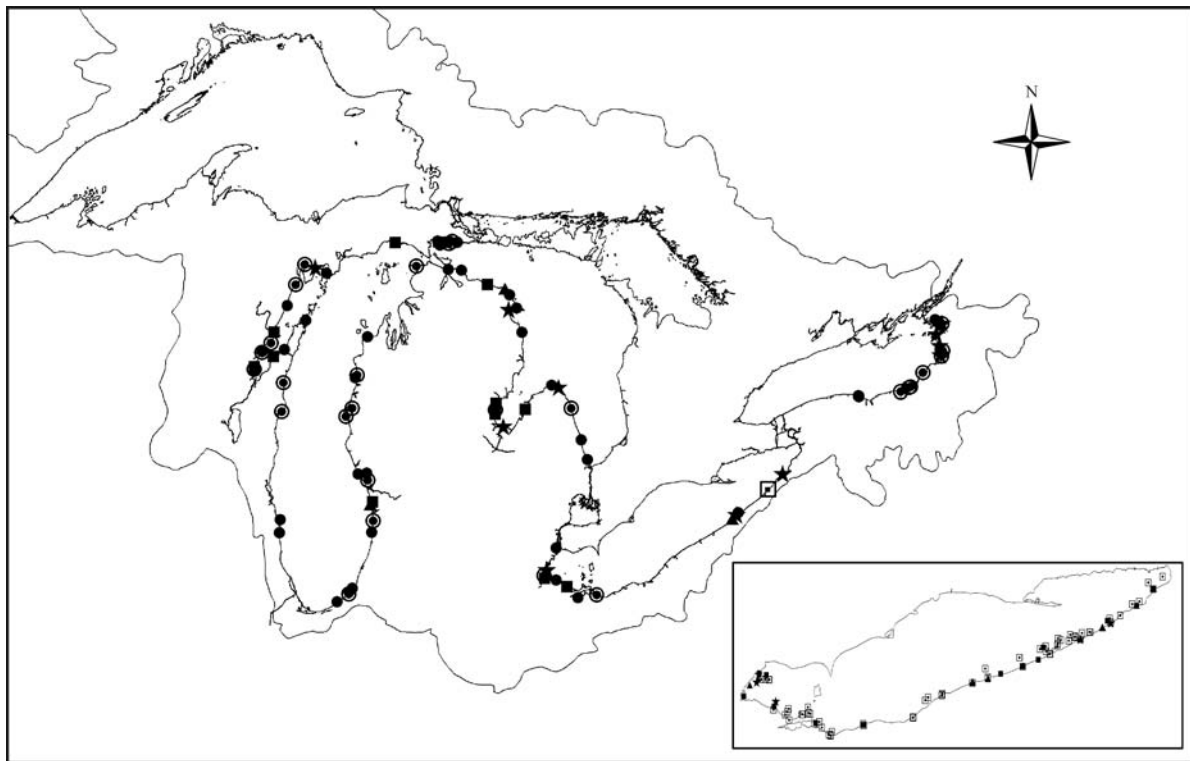


FIG. 1. Distribution of *E. ischnus* (E), *G. fasciatus* (G), and *Dreissena* spp. (D), across the U.S. Great Lakes basin for GLEI and ECCS (inset) sites. Symbols indicate occurrences of E+G+D (★), E+D (▲), E+G (◆), D+G (■), D (○), G (◻), and none of the taxa (●) at sampled sites.

spanned the complete range of most stressor variable PC scores and were not concentrated at specific levels for any of the stressor variables (Fig. 2), as was corroborated by visual examination of scat-

terplots derived from the logistic regression analyses.

The distribution of *E. ischnus* at GLEI sites that supported *G. fasciatus* was independent of the de-

TABLE 2. Number of sites with presence (G only or E only), co-occurrence (E and G), and absence (None) of *E. ischnus* (E) and *G. fasciatus* (G) from GLEI and ECCS data. Significant Yates corrected *p*-values and nonsignificant (ns) associations are indicated.

Scale	E and G	G only	E only	None	Total (n)	p
Basin*	14	40	5	38	97	ns
Michigan*	2	19	2	16	39	ns
Huron*	3	10	1	12	26	ns
Erie	3	4	2	5	14	ns
Ontario	6	7	0	5	18	ns
Coastal wetland*	4	13	0	11	28	ns
Embayment	3	3	1	8	15	ns
High-energy*	4	5	4	17	30	ns
River-influenced	3	19	0	2	24	ns
Microhabitat*	26	237	13	649	925	< 0.0005
ECCS*	5	14	13	64	96	ns

*Scales at which numbers of sites sampled provide suitable α -levels (0.75) for detection of rare species (as per McArdle 1990).

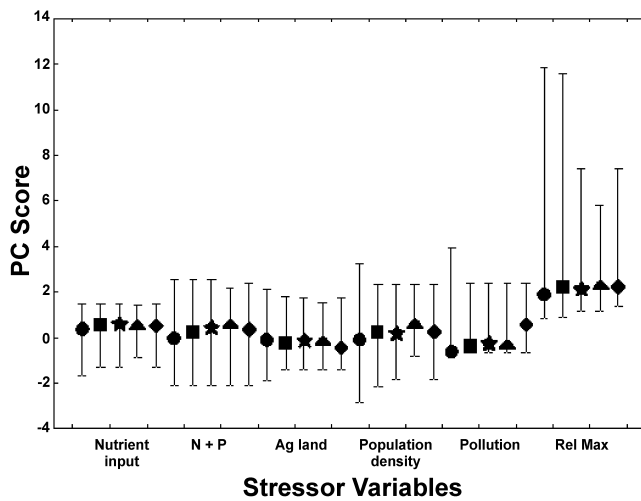


FIG. 2. Ranges of overall nutrient input, N and P load, agricultural land area, human population density, overall pollution loading, and relative maximum stressor variables for all GLEI sites (●), Basin (■), *Echinogammarus* (★), *Gammarus* (▲), and *Dreissena* (◆) sites. Symbols denote median PC Score.

gree of stress for all variables evaluated at the basin, individual lake, and hydrogeomorphic type scales ($p > 0.05$ experiment-wise adjusted for multiple tests). A marginally significant regression was detected for the human population density stressor variable at Lake Erie sites ($\chi^2 = 12.10$, $p < 0.05$ nominal, $n = 7$). However, the sample size for this

analysis was so small that the ordering of *E. ischnus* absences and presences on the stressor axis could have arisen by chance. Analyses of ECCS data, which consisted of more sampling locations, did not corroborate the GLEI Lake Erie results ($p > 0.05$, $n = 19$).

Amphipod-*Dreissena* spp. Co-occurrence

Dreissena spp. were found at 32 of the 97 GLEI sites sampled (33%) (Fig. 1). *E. ischnus* occurred at 56% of the *Dreissena* spp. sites. *E. ischnus* was found without *Dreissena* spp. at only one river-influenced wetland site, in Lake Ontario.

E. ischnus and *Dreissena* spp. co-occurrence was highly significant across many scales (basin: $\chi^2 = 37.35$, $p < 0.001$, $n = 97$; Lake Michigan: $\chi^2 = 10.42$, $p < 0.05$, $n = 39$; Lake Erie: $\chi^2 = 9.98$, $p < 0.05$, $n = 14$; high-energy: $\chi^2 = 13.13$, $p < 0.0005$, $n = 30$; Table 3). None of the 18 ECCS locations at which *Echinogammarus* was found lacked *Dreissena* spp. ($\chi^2 = 89.55$, $p < 0.00005$, $n = 96$) (Table 3).

This association was also significant at the microhabitat scale ($\chi^2 = 169.17$, $p < 0.0005$, $n = 925$; Table 3). *E. ischnus* and *Dreissena* spp. co-occurred in 34 samples collected (2% of all samples), and neither were collected from 787 samples (85% of all samples) out of a total of 925 samples collected. *E. ischnus* was collected in a total of 39 samples (4% of all samples), while *Dreissena* spp. were collected in a total of 114 samples (12% of all sam-

TABLE 3. Number of sites with presence (D only or E only), co-occurrence (E and D), and absence (None) of *E. ischnus* (E) and *Dreissena* spp. (D) from GLEI and ECCS data. Significant Yates corrected p -values, and nonsignificant (ns) associations are indicated.

Scale	E and D	D only	E only	None	Total (n)	p
Basin*	18	14	1	64	97	< 0.0005
Michigan*	4	5	0	30	39	< 0.05
Huron*	4	6	0	16	26	ns
Erie	5	0	0	9	14	< 0.05
Ontario	5	3	1	9	18	ns
Coastal wetland*	4	5	0	19	28	ns
Embayment	4	2	0	9	15	ns
High-energy*	8	4	0	18	30	< 0.0005
River-influenced	2	3	1	18	24	ns
Microhabitat	34	99	5	787	925	< 0.0005
ECCS*	18	0	0	78	96	< 0.00005

*Scales at which numbers of sites sampled provide suitable α -levels (0.75) for detection of rare species (as per McArdle 1990).

TABLE 4. Number of sites with presence (D only or G only), co-occurrence (G and D), and absence (None) of *G. fasciatus* (G) and *Dreissena* spp. (D) from GLEI and ECCS data. Significant Yates corrected *p*-values, and nonsignificant (ns) associations are indicated.

Scale	G and D	D only	G only	None	Total (n)	p
Basin*	26	6	28	37	97	< 0.05
Michigan*	7	2	14	16	39	ns
Huron*	9	1	4	12	26	ns
Erie	5	0	2	7	14	ns
Ontario	5	3	8	2	18	ns
Coastal wetland*	9	0	8	11	28	ns
Embayment	5	1	1	8	15	ns
High-energy*	7	5	2	16	30	ns
River-influenced	5	0	17	2	24	ns
Protected wetland	2	0	2	15	19	ns
Microhabitat	62	52	201	610	925	< 0.0005
ECCS*	19	0	0	77	96	< 0.00005

*Scales at which numbers of sites sampled provide suitable α -levels (0.75) for detection of rare species (as per McArdle 1990).

ples). *E. ischnus* was not associated with *Dreissena* spp. in five samples collected from a single river-influenced wetland site in eastern Lake Ontario, which did not score highly for any stressor variable. Otherwise, every GLEI D-net, core, and Petite Ponar sample containing *E. ischnus* also contained *Dreissena* spp.

G. fasciatus and *Dreissena* spp. co-occurred at 27% of all sampled sites (Table 4). The association between *G. fasciatus* and *Dreissena* spp. was significant at the basin ($\chi^2 = 11.16$, $p < 0.05$, $n = 97$) and microhabitat ($\chi^2 = 41.60$, $p < 0.0005$, $n = 925$) scales (Table 4). ECCS data showed that *G. fasciatus* and *Dreissena* spp. co-occurrence was highly significant ($\chi^2 = 89.80$, $p < 0.00005$, $n = 96$).

DISCUSSION

At the hydrogeomorphic type scale, *G. fasciatus* appeared to be more widespread among river-influenced wetlands than among high energy shorelines or in embayments. In contrast, *Echinogammarus* was twice as frequently encountered at the high-energy and embayment sites than in the wetlands. However, this may be more a reflection of the relative distribution of hydrogeomorphic types among Great Lakes, which were sampled with equal effort rather than by actual habitat occurrence. For example, *Echinogammarus* was most prevalent in Lake Erie, where there were a disproportionately large number of high-energy sites and relatively few

river-influenced wetland sites sampled. The highly significant association between the two amphipod species at the sample scale suggests that microhabitat preferences are similar. Although the small sample size of *E. ischnus* sites does not provide conclusive evidence for a difference in habitat (hydrogeomorphic) preferences, this study and others (Palmer and Ricciardi 2004, Palmer and Ricciardi 2005, Limen *et al.* 2005) suggest that *E. ischnus* is not systematically replacing *G. fasciatus* in the Great Lakes. Differential resource use (Limen *et al.* 2005), and differential responses to substrate characteristics, water chemistry variables, and current velocity (Palmer and Ricciardi 2004, Palmer and Ricciardi 2005) are evidence that *E. ischnus* can utilize different microhabitat from *G. fasciatus*. Alternatively, although *E. ischnus* has been reported from all of the Great Lakes, the patchiness in occurrences among lakes and hydrogeomorphic types may reflect its limited dispersal capabilities and relatively recent introduction, resulting in insufficient time to disperse throughout the lakes.

Overall, the presence or absence of *E. ischnus* at *G. fasciatus* sites was independent of the degree of anthropogenic stress. The Holm (1979) correction used to adjust the detection level for significance to correct for inflated Type I Error from the many simple logistic regression analyses, rendered several of what would have been nominally significant ($p < 0.05$) relationships nonsignificant. Ultimately, the only simple logistic regression analysis of

E. ischnus presence/absence found to be marginally significant at the experiment-wise corrected probability level was for the human population density stressor variable at GLEI Lake Erie *G. fasciatus* sites. Since this analysis was based on a small sample size ($n = 7$) with a marginally significant likelihood of getting the observed significant results by chance ($p < 0.03$), it imparts weak support at best for the disturbance hypothesis. The ECCS Lake Erie data, for which more records of *E. ischnus* were observed, did not corroborate the GLEI Lake Erie results.

The distribution of dreissenids, which co-occurred with *E. ischnus* at numerous scales, appeared to determine the distribution of the nonindigenous amphipod more consistently than stressors or the distribution of *G. fasciatus*. This finding across such a broad geographic range suggests that dreissenids may regulate the distribution of *E. ischnus* from broad to microhabitat scales, illustrating the importance of facilitative interactions for NIS success. If this is the case, *E. ischnus* may eventually inhabit protected wetland sites if it is able to disperse to those areas where *Dreissena* spp. also occur. The NIS occupy the same native habitat of the Ponto-Caspian region, and it is speculated that co-evolution with dreissenids has assisted *E. ischnus* establishment in the Great Lakes (Dermott *et al.* 1998, van Overdijk *et al.* 2003). Studies have predicted (Witt *et al.* 1997) or demonstrated (Dermott *et al.* 1998, Stewart *et al.* 1998, Burkart 1999) replacement of *G. fasciatus* by *E. ischnus* on *Dreissena* substrata in the Great Lakes. This replacement of *G. fasciatus* by *E. ischnus* may be related to the stronger affinity of the latter for substrata fouled by *Dreissena*. Conversely, increases in *G. fasciatus* abundances have also been predicted as a consequence of the *Dreissena* spp. invasion (Griffiths 1993, Stewart and Haynes 1994). Field and laboratory studies revealed that *E. ischnus* preferred *Dreissena*-encrusted rocks more than *Cladophora*-encrusted rocks, whereas *G. fasciatus* used both substrata (van Overdijk *et al.* 2003).

The distribution of *G. fasciatus* was also significantly associated with that of dreissenids but not as strongly as the association between *E. ischnus* and *Dreissena* spp. Forty-eight percent of the sites at which *G. fasciatus* were collected did not support dreissenids. Thus, although they often co-occur across the basin, *G. fasciatus* are not regulated by dreissenids. (Table 4). Furthermore, *G. fasciatus* were well established in the Great Lakes decades before the arrival of dreissenids (Mills *et al.* 1993).

Because of its relatively recent arrival in North America, the distribution of *E. ischnus* across the Great Lakes would be expected to reflect the propagule pressure imparted from ballasting activities of transoceanic ships and recreational boating (Ricciardi and MacIsaac 2000). However, this seems not to be the case for *E. ischnus*. The results of our heterogeneity tests and comparisons with expected frequencies show a higher proportion of *E. ischnus* and *Dreissena* spp. occurrences at Lakes Erie and Ontario sites than for the other lakes (Table 1). In contrast, *E. ischnus* did not appear in Lake Superior samples, even though Duluth and Thunder Bay harbors (Lake Superior) receive a disproportionate number of visits by transoceanic ballasted and NOBOB vessels (ships with no-ballast-on-board status) compared to other ports of the Great Lakes (Colautti 2001). In general, Duluth and Thunder Bay support few NIS in their vicinity (Grigorovich *et al.* 2003). Lakes Erie and Ontario may provide better environmental conditions for mesothermic NIS entering the basin than the other Great Lakes (Vanderploeg *et al.* 2002, Grigorovich *et al.* 2003).

Results from this study do not support the disturbance hypothesis (increased likelihood of establishment at location in which stress has disrupted normal interaction among species comprising the natural community), and are more consistent with the environmental suitability hypothesis (NIS become established wherever conditions are adequate). Anthropogenic stressors at Great Lakes coastal margins do not appear to facilitate nonindigenous benthic invertebrate establishment, as exemplified by *E. ischnus*. Our results and those of others (Levine and D'Antonio 1999, Blackburn and Duncan 2001, Holway, *et al.* 2002, Dethier and Hacker 2005) suggest that the same environmental properties that provide suitable habitat for native species are also invisable for NIS.

Relatively sessile benthic macroinvertebrates are the closest animal equivalent to terrestrial plant communities, where disturbance often does increase invasibility. However, this study suggests that disturbance does not factor into aquatic invertebrate invasion processes as it does with terrestrial plants. Aquatic habitats are thought to be highly vulnerable to invasions (Mills *et al.* 1993) due to their generally low level of native species diversity and high level of invasion opportunities. However, few studies test this assertion due to the difficulty in directly linking and assessing the contribution of disturbance to NIS success. Movement into potential

habitats and dispersal limitations may be the primary obstacles for aquatic invasions (Levine 2000), but this does not explain why relatively few of the aquatic NIS that arrive in a new habitat establish viable populations. Factors such as habitat match (Kolar and Lodge 2001, Moyle and Light 1996), phenotypic plasticity (Crawley 1987), propagule pressure (Levine 2000, Lockwood *et al.* 2005, Von Holle and Simberloff 2005), facilitative interactions (Simberloff and Von Holle 1999, Ricciardi 2001, Bruno *et al.* 2003), and life history requirements of NIS that inhibit establishment success (Fausch *et al.* 2001) are almost certainly involved. Further studies attempting to elucidate the disparity between the dependence of plant and animal NIS on disturbance for establishment would be helpful in understanding the dynamics of invasion biology, particularly for aquatic environments.

CONCLUSIONS

We did not find any consistent association between *E. ischnus* distribution in the Great Lakes and degree of stress contributed from the land to drainage basin-scale habitats. Our results do not support the hypothesis that invasion is more likely to occur in locations influenced by the types of stressors examined in this study. *E. ischnus*' presence at sites that are subject to varying intensities and types of stressors across the Great Lakes basin suggests that this NIS occurs wherever environmental conditions are suitable and that are concurrently occupied by *Dreissena* spp., giving precedence to the environmental suitability hypothesis over the disturbance hypothesis as an explanation for the distribution of *Echinogammarus* at Great Lakes coastal margins.

ACKNOWLEDGMENTS

Over 40 technical staff and research assistants from universities of Minnesota Duluth, Windsor, and Wisconsin-Superior participated in the collection and subsequent sorting of samples used in this analysis over four years. We are especially indebted to Dan Breneman, Anh Ly, Robert Hell, Jesse Bailargeon, Joseph Gathman, and Rachael Eedy. We thank Valerie Brady and Tom Hollenhorst for their assistance with data compilation and analysis. Igor Grigorovich confirmed the identity of amphipods. Jeff Schuldt and Carl Richards contributed significantly to the overall GLEI zoobenthic study design. We also thank David R. Barton and Kenneth A.

Krieger for their willingness to share amphipod and dreissenid data collected and compiled from the ECCS study.

This research was supported by grants from the U.S. Environmental Protection Agency's Science to Achieve Results Estuarine and Great Lakes Coastal Initiative through funding to the Great Lakes Environmental Indicators project, U.S. EPA Agreements EPA/R-8286750 and EPA/R-82877701. The ECCS data were collected with the support of grants from the U.S. Environmental Protection Agency, Environment Canada, and Ontario Ministry of the Environment to J. Ciborowski, K. Kreiger, and D. Barton. Other funding was provided by grants from the Natural Sciences and Engineering Research Council of Canada to J. Ciborowski, and Ontario Graduate Scholarship in Science and Technology to M. Kang. This is contribution number 466 for the Center for Water and the Environment at the Natural Resources Research Institute, University of Minnesota Duluth.

REFERENCES

- Baltz, D.M., and Moyle, P.B. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecol. Appl.* 3:246–255.
- Barton, D.R., and Hynes, H.B.N. 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. *J. Great Lakes Res.* 4:27–45.
- Bially, A., and MacIsaac, H.J. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwater Biol.* 43:85–97.
- Blackburn, T.M., and Duncan, R.P. 2001. Determinants of establishment success in introduced birds. *Nature* 414:195–197.
- Bousfield, E.L. 1958. Fresh-water amphipod crustaceans of glaciated North America. *Can. Field Nat.* 72:55–113.
- Bruno, J.F., Stachowicz, J.J., and Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18:119–125.
- Burkart, G.A. 1999. Zebra mussel mediation of habitat use by native and exotic amphipods: importance of food availability and predation risk. MSc. thesis, Wright State University, Dayton, Ohio.
- Burke, M.J.W., and Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77:776–790.
- Case, T.J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biol. Conserv.* 78:69–96.
- Ciborowski, J.J.H. 1991. Estimating processing time of stream benthic samples. *Hydrobiologia* 222:101–107.
- Clemens, H.P. 1950. Life cycle and ecology of *Gam-*

- marus fasciatus* Say. Contrib. Stone Lab. Ohio Univ. 12:1–63.
- Cohen, A.N., and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558.
- Colautti, R. 2001. Spatial and temporal analysis of transoceanic shipping vectors to the Great Lakes. Undergraduate thesis, University of Windsor, Windsor, Ontario.
- Covich, A.P., and Thorp, J.H. 2001. Introduction to the subphylum Crustacea. In *Ecology and classification of North American freshwater invertebrates, second edition*, J.H. Thorp and A.P. Covich, eds., pp. 777–809. San Diego, California: Academic Press.
- Crawley, M.J. 1987. Benevolent herbivores. *Trends Ecol. Evol.* 2:167–168.
- Csanady, G.T., and Scott, J.T. 1974. Barocline coastal jets in Lake Ontario during IFYGL. *J. Phys. Oceanog.* 4:524–541.
- Dahl, J.A., Graham, D.M., Dermott, R., Johannsson, O.E., Millard, E.S., and Myles, D.D. 1995. *Lake Erie 1993, western, west-central, and eastern basins; changes in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels*. Can. Tech. Rep. Fish. Aquat. Sci. 2070.
- D'Antonio, C.M. 1993. Mechanisms controlling invasion of coastal plant-communities by the alien succulent *Carpobrotus-Edulis*. *Ecology* 74:83–95.
- Danz, N., Regal, R., Niemi, G.J., Brady, V.J., Hollenhorst, T., Johnson, L.B., Host, G.E., Hanowski, J.M., Johnston, C.A., Brown, T., Kingston, J., and Kelly, J.R. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. *Environ. Monit. Assess.* 102:41–65.
- Dermott, R., Witt, J., Um, E.M., and Gonzalez, M. 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. *J. Great Lakes Res.* 24:442–452.
- Dethier, M.N., and Hacker, S.D. 2005. Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. *Ecol. Appl.* 15:1273–1283.
- Drake, J.A., Mooney, H.A., di'Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., and Williamson, M.W. 1989. *Biological invasions: a global perspective*. New York, New York: John Wiley & Sons.
- Elton, C. 1958. *The ecology of invasions by animals and plants*. London, United Kingdom: Chapman and Hall.
- Fausch, K.D., Taniguchi, Y., Nakano, S., Grossman, G.D., and Townsend, C.R. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecol. Appl.* 11:1438–1455.
- Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. In *Zebra mussels: biology, impacts, and control*, T.F. Nalepa and D. Schloesser, eds., pp. 415–437. Boca Raton, Florida: Lewis Publishers.
- Grigorovich, I.A., Kornushin, A.V., Gray, D.K., Dugan, I.C., Colautti, R.I., and MacIsaac, H.J. 2003. Lake Superior: an invasion coldspot? *Hydrobiologia* 499:191–210.
- , Kang, M., and Ciborowski, J.J.H. 2005. Colonization of the Laurentian Great Lakes by the amphipod *Gammarus tigrinus*, a native of the North American Atlantic coast. *J. Great Lakes Res.* 31:333–342.
- Harrison, S. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* 121:99–106.
- Hobbs, R.J., and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6:324–337.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6:65–70.
- Holsinger, J.R. 1976. *The freshwater amphipod crustaceans (Gammaridae) of North America*. Cincinnati, Ohio: U.S. EPA.
- Holway, D.A., Suarez, A.V., and Case, T.J. 2002. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology* 83:1610–1619.
- Hood, W.G., and Naiman, R.J. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology* 148:105–114.
- Keane, R.M., and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17:164–170.
- Keeley, J.E., Lubin, D., and Fotheringham, C.J. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.* 13:1355–1374.
- Keough, J.R., Thompson, T.A., Guntenspergen, G.R., and Wilcox, D.A. 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. *Wetlands* 19:821–834.
- Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 18:199–204.
- Kotaniemi, P.M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. *J. Applied Ecology* 34:631–644.
- Krieger, K.A., Bur, M.T., Ciborowski, J.J.H., Barton, D.R., and Schloesser, D.W. 2007. Distribution and abundance of burrowing mayflies (*Hexagenia* spp.) in Lake Erie: value as a lake quality indicator. *J. Great Lakes Res.* 33 (Suppl. 1):20–33.
- Levine, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854.
- , and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.

- Limen, H., van Overdijk, C.D.A., and MacIsaac, H.J. 2005. Food partitioning between the amphipods *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* as revealed by stable isotopes. *J. Great Lakes Res.* 31:97–104.
- Lockwood, L., Cassey, P., and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20:223–228.
- MacIsaac, H.J., Grigorovich, I.A., and Ricciardi, A. 2001. Reassessment of species invasion concepts: the Great Lakes basin as a model. *Biol. Invasions* 3:405–416.
- McArdle, B.H. 1990. When are rare species not there? *Oikos* 57:276–277.
- Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes—a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19:1–54.
- Mooney, H.A., and Drake, J.A. 1986. *Ecology of biological invasions of North America and Hawaii*. New York, New York: Springer-Verlag.
- Moyle, P.B., and Light, T. 1996. Fish invasions in California: do abiotic factors determine success? *Ecology* 77:1666–1670.
- Nalepa T.F., Schloesser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., and Fleischer, G.W. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *J. Great Lakes Res.* 27:384–391.
- Palmer, M.E., and Ricciardi, A. 2004. Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. *Can. J. Zool.* 82:1886–1893.
- , and Ricciardi, A. 2005. Community interactions affecting the relative abundances of native and invasive amphipods in the St. Lawrence River. *Can. J. Fish. Aquat. Sci.* 62:1111–1118.
- Rose, M., and Hermanutz, L. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. *Oecologia* 139:467–477.
- Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Can. J. Fish. Aquat. Sci.* 58:2513–2525.
- , and MacIsaac, H.J. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends Ecol. Evol.* 15:62–65.
- Sax, D.F., Stachowicz, J.J., and Gaines, S.D. 2005. *Species Invasions: Insights into Ecology, Evolution and Biogeography*. Sunderland, Massachusetts: Sinauer Associates.
- Schreiber, E.S.G., Quinn, G.P., and Lake, P.S. 2003. Distribution of an alien aquatic snail in relation to flow variability, human activities and water quality. *Freshwater Biol.* 48:951–961.
- Simberloff, D., and Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1:21–32.
- Simons, T.J. 1976. Continuous dynamical computations of water transport in Lake Erie for 1970. *J. Fish. Res. Board Can.* 33:371–384.
- StatSoft, Inc. 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.
- Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. *J. Great Lakes Res.* 20:479–493.
- , Miner, J.R., and Lowe, R.L. 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. *J. Great Lakes Res.* 24:868–879.
- Valentine, J.P., and Johnson, C.R. 2003. Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. *J. Exp. Mar. Biol. Ecol.* 295:63–90.
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 59:1209–1228.
- van Overdijk, C.D.A., Grigorovich, I.A., Mabee, T., Ray, W.J., Ciborowski, J.J.H., and MacIsaac, H.J. 2003. Microhabitat selection by the invasive amphipod *Echinogammarus ischnus* and native *Gammarus fasciatus* in laboratory experiments and in Lake Erie. *Freshwater Biol.* 48:567–578.
- Von Holle, B., and Simberloff, D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218.
- White, P.S., and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. In *The ecology of natural disturbance and patch dynamics*, S.T.A. Pickett, P.S. White, eds., pp. 3–13. Orlando, Florida: Academic Press.
- Wiser, S.K., Allen, R.B., Clinton, P.W., and Platt, K.H. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79:2071–2081.
- Witt, J.D.S., Hebert, P.D.N., and Morton, W.B. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. *Can. J. Fish. Aquat. Sci.* 54:264–268.

Submitted: 14 September 2006

Accepted: 12 July 2007

Editorial handling: Gerald J. Niemi